

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 2861, pp. 1–8, figs. 1–9
October 31, 1986

The Natural History of the Old World Nomadine Parasitic Bee *Pasites maculatus* (Anthophoridae: Nomadinae) and Its Host *Pseudapis diversipes* (Halictidae: Nomiinae)

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ABSTRACT

In nests of *Pseudapis diversipes* in Pakistan, a series of branching tunnels surrounded vertical cells clustered close to one another in the ground. Information on the tunnel and cell walls, cell size, eggs, and provisions is given. The cuckoo bee *Pasites maculatus* flew around the nest entrances; its eggs and first instars were recovered from host cells. Information on oviposition and egg size and structure is presented. The first instar had large

sickle-shaped mandibles used to eliminate the host larva (or egg) and rival cuckoo bee larvae, as is the case with other nomadine parasitic bees. *Pasites* (Old World) and *Oreopasites* (New World) both deposit eggs that are folded into a U as they are inserted into the cell wall. This form of oviposition, a unique feature in the Apoidea, suggests a close relationship between the two genera.

INTRODUCTION

Recently in Pakistan I discovered nests of a *Pseudapis* being visited by cuckoo bees of the genus *Pasites*. Donald B. Baker kindly identified the host as *Pseudapis diversipes* (Latreille) (Halictidae: Nomiinae) and the

cleptoparasite as *Pasites maculatus* Jurine (Anthophoridae: Nomadinae). The literature reveals little information on the nesting biology of the host and on the mode of parasitism by *Pasites*. The following provides

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some specific data about these bees and permits a comparison of the biology of *Pasites* with that of other *Nomadinae*.

The association of *Pasites maculatus* with *Pseudapis diversipes* and perhaps with other *Pseudapis* has been recorded in the European literature for nearly a century. Recently, Hirashima and Nagase (1981) have associated *Pasites esakii* Popov and Yasumatsu with *Pseudapis mandschurica* (Hedicke) in Japan.

Pseudapis, previously regarded as a sub-genus of *Nomia*, has recently been accorded generic status (Baker, personal commun.; Hirashima, 1961; Hirashima and Nagase, 1981; Michener, personal commun.). Its numerous species extend from Europe to southern Africa and to Japan (Michener, 1961), and into the Indian region and Indochina (Baker, personal commun.). *Pasites*, consisting of only a few nominal species, ranges from Europe and North Africa to Japan (Popov, 1931; Hirashima and Nagase, 1981). Information on the genus is limited, and the usage of various infraspecific names (see, for example, Hirashima and Nagase, 1981) suggests that a more thorough study of the genus over its entire geographic range may lead to a larger number of species and a more convincing taxonomy.

Donald B. Baker (in litt.) sent me his notes on *Pasites maculatus* and its host. They provide an informative overview of the taxonomic problems with this cuckoo bee, paralleling those I have had with the North American ammobatine *Oreopasites*.

The range of *Pasites maculatus* extends from Northwest Africa to Japan. From Spain to Central Asia and Pakistan its certain principal host (and its probable principal host further afield, but not everywhere) is *Pseudapis diversipes* (Latr.). I have examined several thousand specimens of the host species, which shows rather little geographical variation (as one might expect in a species that has a more or less continuous distribution and which usually occurs abundantly wherever it is found: I have the impression that clinal variation tends to be more marked in species that have a more scattered distribution and smaller populations). I have examined some hundreds of specimens of the *Pasites*, which shows considerable variation in size and in colour, pubescence, sculptural and, to a comparatively small extent, structural char-

acters. Variation may be extensive within populations (the species is rarely taken in numbers and appears always to be much less numerous than its host; I have never observed gradation), and, generally, variants within one population can be matched by variants within other, distant, populations.

Pasites maculatus may, as you suggest, be composite, but I cannot satisfactorily divide it on the basis of the material I have seen, and I do not think the question will be resolved until we have adequate series of specimens from known hosts from a number of localities: host data are lacking for almost all museum specimens, and host identities can rarely be inferred from collection data since the species of *Pseudapis* are numerous and since several species may commonly be found flying together within one locality. (Even within the large area where *Pseudapis diversipes* is probably the sole host of *maculatus*, variability of the latter is considerable; but under these circumstances one would hardly expect the variation to indicate the presence of more than one species of parasite.)

ACKNOWLEDGMENTS

Ronald J. McGinley, Smithsonian Institution, Sarfraz Lodhi, American Museum of Natural History, and Ian Stupakoff, City University of New York, participated on this trip and aided in sampling the bee fauna at this nesting site.

I thank the following persons for carefully reviewing this manuscript: Donald B. Baker, Surrey, England; G. E. Bohart, Logan, Utah; and Charles D. Michener, Lawrence, Kansas.

The following individuals and their institutions assisted us in various ways in fulfilling this and other studies on Pakistan bees: Dr. Rafiq Ahmad, National Coordinator, Honeybee Research Programme, Pakistan Agricultural Research Council, Islamabad, Pakistan; Dr. Manzoor Ahmed, Department of Zoology, University of Karachi, Pakistan; Dr. Abdul Hameed Bajoi, Entomologist, Agricultural Research Institute, Quetta; and Dr. Riaz Ali Shah, Director General, Pakistan Museum of Natural History, Islamabad. The field trip was made possible through the support of the Smithsonian Institution's Foreign Currency Program and I thank Dr. Gretchen Ellsworth, Director, Office of Fellowships and Grants, at the Smithsonian, and her staff for assisting me in obtaining the support.



Fig. 1. Nesting area of *Pseudapis diversipes* at Jalogir, 32 km north of Quetta, Baluchistan, Pakistan. Ronald J. McGinley examining nest entrances in pathway in front of adobe wall.

NESTING BIOLOGY OF *PSEUDAPIS DIVERSIPES*

I found three nests, possibly interconnected, within 25 cm of one another on May 16, 1984, at Jalogir, 32 km north of Quetta, Baluchistan, Pakistan. I hastily excavated two of the nests, recovered immatures of both hosts and cuckoo bees, made brief notes on nest architecture, and preserved samples of cells and immatures for possible future study. The nest entrances occurred on a packed dirt pathway with loose surface soil next to an adobe wall surrounding an agricultural field (fig. 1) containing many flowering thistles, the possible food source of *Pseudapis*. The sub-surface soil was fine and had no rocks and little organic material. Nest entrances were unshaded by vegetation for most of the day. At least three females were associated with one nest.

The main tunnel (5.0 mm in diameter) of one nest descended obliquely into the horizontal surface and at a depth of 2 cm became vertical, branched at about the depth of 5 cm near a single cell, and then continued to descend vertically to the depth of 15 cm. At this level it divided into a number of horizontal branches that extended in various directions, abruptly turned downward and then apparently coalesced so that the branches enclosed

a central area that was perhaps 5–8 cm horizontally and 3 cm vertically. The vertical cells, one next to another, were clustered in this enclosed area. Similar clusterings have been reported for both the Nomiinae and the Halictinae with the open area surrounding the cluster varying from tunnels (as here) to a mostly open chamber with a few earthen pillars supporting the cluster (Stephen et al., 1969; Hirashima, 1961). A single nest may have included more than one such cluster (as reported by Hirashima, 1961, for *Nomia* (*Hoplonomia*) *punctulata* Dalla Torre) and possibly other cells not in clusters. Nest architecture was not studied in detail and obviously deserves further investigation.

The second nest excavated consisted of a burrow of about the same diameter descending nearly vertically to the depth of about 6 cm at which point it started to branch, as was the case with the first nest.

The walls of branches were rough with numerous indentations created by the females' tamping the walls with their pygidial plates (fig. 3). The impression of the median carina on the pygidial plate was clearly identifiable in each embossing (fig. 4). The walls, uncoated, absorbed water droplets immediately.

All cells (figs. 2, 9) were vertical, closure

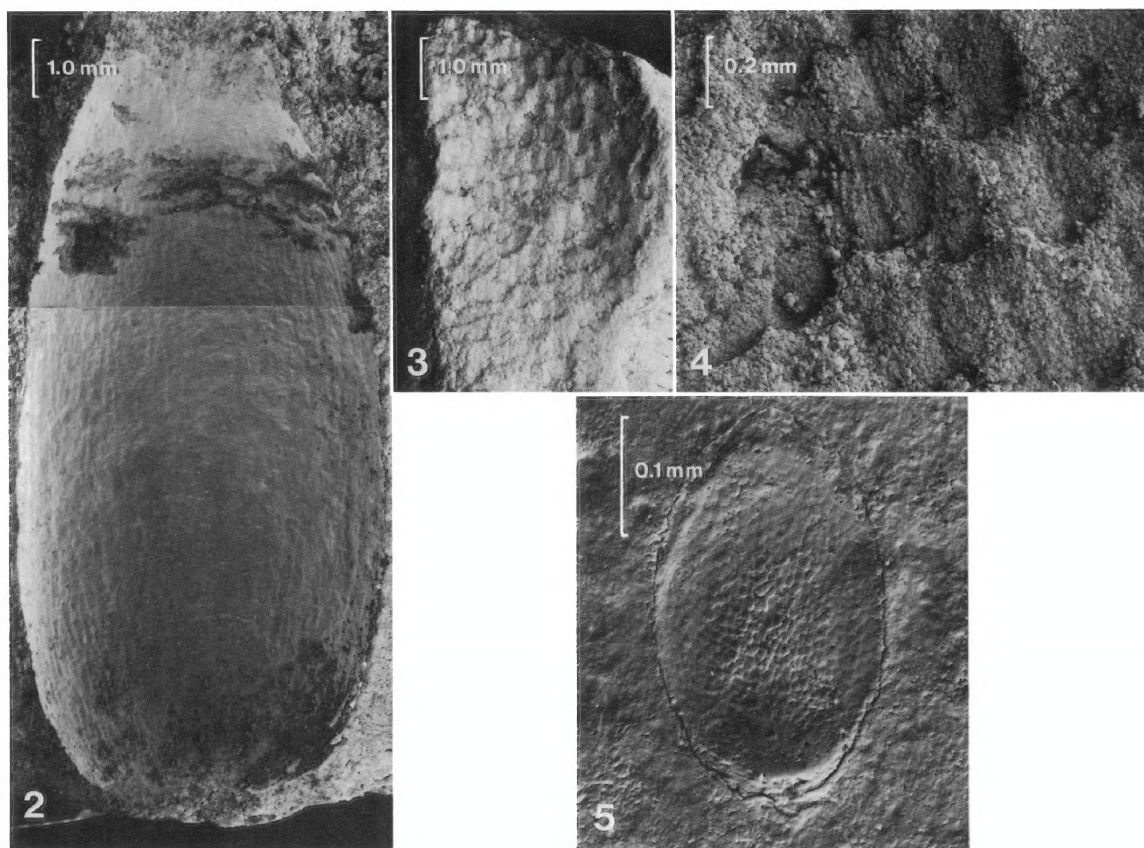


Fig. 2. Composite scanning micrograph of open cell of *Pseudapis diversipes* showing faint waves in cell wall and scratches near top of cell probably created by female *Pseudapis* attempting to remove *Pasites* egg; hole on right side thought to be puncture created by insertion of *Pasites* egg that later was destroyed by *Pseudapis* female.

Fig. 3. *Pseudapis diversipes*, scanning micrograph of section of tunnel circumscribing cell cluster, showing embossings created by pygidial plate of female.

Fig. 4. Same, more highly magnified; note median line created by median carina on pygidial plate.

Fig. 5. *Pasites maculatus*, scanning micrograph of operculum embedded in cell wall of *Pseudapis diversipes*.

end up, and spaced close to one another so that intervening distances ranged from 1.5 to 3.0 mm (seven measurements). Distances between cells and the descending burrows varied from 3.0 to 6.0 mm (seven measurements). Such figures give an indication of the compactness of the cell cluster. Cell length ranged from 10.5 to 11.0 mm from cell bottom to outer rim of spiral cell closure (three measurements); maximum cell diameter, 5.7 to 6.0 mm (nine measurements); and diameter at the closure, 3.5 to 3.8 mm (four measurements). They were symmetrical about their long axes, unlike many bee cells, and possessed a conspicuous, shiny, semitrans-

parent lining that could be peeled in sections from the wall. The lining was waterproof when tested with a water droplet, and extended over the entire inner surface of the cell. The wall exhibited a pattern of vertical waves (fig. 2) over the entire surface, and was similar in hardness and texture to the surrounding substrate.

In each of three cells the wall had been built into a vacated cell from which a larva had matured (fig. 8). The fecal material and exuviae, as well as some soil, were in the bottom of the old cell and a new cell bottom was plastered over the old remains. The side walls of the old and new cells met part way up

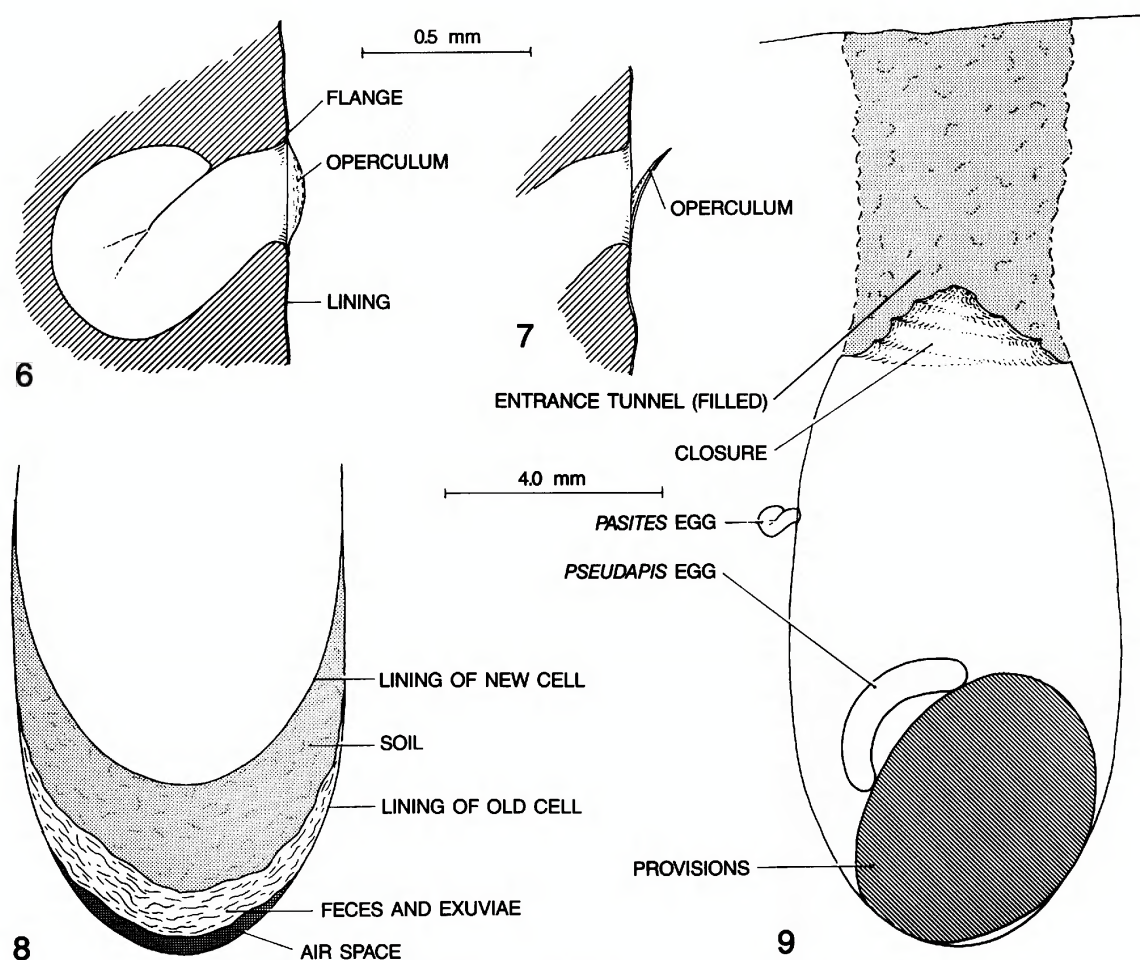


Fig. 6. *Pasites maculatus*, egg, side view, inserted in wall of cell of *Pseudapis diversipes*.

Fig. 7. Same, anterior part of chorion showing operculum open as a result of egg hatching, side view.

Fig. 8. *Pseudapis diversipes*, bottom part of new cell constructed in old cell in which the previous generation had developed, side view.

Fig. 9. Same, entire cell containing provisions, egg, and egg of *Pasites maculatus*, side view.

Scales refer to figs. 6–7 and 8–9, respectively.

without showing any sign of meeting on the surface; the transparent cell lining seemed continuous. The plastered walls of the new cells did not differ from the walls of other cells in which there had been no previous generation, suggesting that females somehow construct walls of all cells by plastering.

The cell closure (fig. 9) was a deeply concave spiral with approximately four coils. When tested with water droplets its inner surface, nonwaterproof, absorbed the moisture immediately. There was no distinct outer surface to the closure (in contrast to the closures

of some taxa in which there is a smooth concave outer surface). The closure material fused completely with the substrate so that, once plugged, the entrance could not be identified.

The entrance tunnels (fig. 9), all vertical and in line with the long axes of the cells, were short (4 to 5 mm long in three cases) and I could not detect where they contacted the horizontal burrows on top of the cell cluster.

The provisions (fig. 9) appeared as flattened smooth spheres (maximum diameter a little more than 5 mm and minimum di-

ameter perhaps 4 mm). The upper surfaces (on which the eggs were found) may have been somewhat flatter than the lower surfaces, but details of exact shape and size were not recorded. Shapes of food masses in the Nomiinae vary from species to species (Cross and Bohart, 1960; Stephen et al., 1969), and should be carefully recorded. The provisions consisted of moist pollen and were angled obliquely in the cell as in figure 9, not unlike that of *Nomia* (*Acunomia*) *melanderi* Cockereil (Stephen et al., 1969).

Large, elongate, whitish eggs were 2.7–3.0 mm long and 0.6 mm in maximum diameter (four measurements) (fig. 9), strongly arched, and attached at each end to the food surface. The transparent chorion seemed moderately smooth and shiny. In two eggs in which the tissue had differentiated, the embryos had their ventral sides directed upward, indicating that they would rotate 180° before hatching as is generally (but not universally) the case with Hymenoptera.

Larvae were in various stages of development and one was already defecating. They deposited feces at the cell bottom, at least in old cells (fig. 8), and did not start defecating until they had finished feeding. Larvae of this genus do not spin cocoons, and their labio-maxillary regions are reduced as is characteristic of noncocoon-spinning bee larvae. On or before May 25, several mature forms that had been kept alive defecated and soon pupated, probably an indication of more than one generation a year. New cells being constructed in vacated cells suggests that a nest is occupied for more than one generation.

BIOLOGY OF *PASITES MACULATUS*

We collected a number of adults of *Pasites maculatus* in the vicinity of the nest entrance. In one *Pseudapis* cell one or more cuckoo bees had deposited three eggs, one of which was still unhatched. The same cell contained a live *Pasites* first instar and a dead one on top of the dead host larva that had been killed as it was about to molt, as indicated by the pharate condition of the mandibular apices. Apparently, the first *Pasites* to hatch had killed the host larva and then had been assassinated by the second *Pasites* to emerge.

Three additional cells each contained an

unhatched *Pasites* egg in the wall; one of the cells had not yet been closed by the host female. Two eggs were 4.0 mm and the other 7.0 mm from the cell bottom.

Eggs (figs. 6, 7) were embedded in the cell wall so that their flanged and obliquely flattened anterior ends (opercula) were flush with the cell walls. They were very small by comparison with the host egg (fig. 9). In each case the operculum (fig. 5) was oval rather than circular. The operculum of the unhatched egg preserved in Kahles solution was 0.33 mm in maximum diameter and 0.23 mm in minimum diameter; opercula of vacated or dried eggs were 0.27–0.29 mm in maximum diameter and 0.18–0.20 mm in minimum diameter (five measurements). The operculum of the egg preserved in Kahles bulged slightly (fig. 6), whereas the others were nearly flat (fig. 5). Each operculum was surrounded by a narrow flange that adhered closely to the cell lining. Although the flange was not clearly evident in the scanning micrograph (fig. 5) because the specimen was coated with metal, it was optically differentiated from the operculum on an uncoated specimen. The unhatched egg preserved in fluid was folded into a U (fig. 6) as is characteristic of *Oreopasites* (Rozen in Bohart, 1970), and the two vacated chorions retained this same shape. Each operculum had a minutely dented surface (fig. 5). Whereas the opercula and flanges were slightly tannish, the rest of the egg chorions were essentially colorless and semitransparent. At hatching, the operculum separated from the flange so that the vacated egg cases had an oval opening with the operculum attached at one point (fig. 7). No larval cast skins were seen in either of the two vacated chorions, whereas with some nonparasitic anthophorids (e.g., Rozen, 1984) there is a strong suggestion that the first instar remains in the same position as the egg and that the second instar is the first to crawl. Evidence suggests, therefore, that the true first instar *Pasites* crawls away from the egg.

Pasites, like other Nomadinae, has an active, rapacious, linear, white first instar that crawls with the aid of a bilobed process at the posterior tip of the abdomen. Only the sclerotized head capsule with a defined dorsal median ecdysial line is pigmented. Prognathous and bearing two elongate labral tuber-

cles, the head is equipped with slender, curved, elongate mandibles and well-developed maxillary palpi. Presumably, the labral tubercles and maxillary palpi assist in locating the immature host and sibling rivals; the mandibles are used to kill hosts and rivals. The antennae and labial palpi are inconspicuous. Thus, the larva is similar in appearance to that of *Oreopasites* (Rozen, 1954).

A number of cells exhibited irregular scratch marks in the wall often associated with a deep puncture (fig. 2). The scratches probably resulted from a host female trying to search for and eliminate *Pasites* eggs with her mandibles; the punctures were the insertion holes of *Pasites* eggs that had been found and destroyed.

Because my field observations on *Pasites* and its host were made in one day, they do not address seasonal phenology. Donald B. Baker collected data pertaining to this matter on the Caspian coastal plain at Tiltrudsar (Iran: Mazandaran, between Chalus and Shahsavari) from 1965 to 1967. His data show that *Pseudapis* flies from May into November, and that there may be two generations a year with females predominating in late summer. His data also reveal that *Pasites maculatus* was present from July 10 to 24 and from August 22 to September 26. My experience with cuckoo bees suggests that adults in a population are active for only a month and a half, and, therefore, *Pasites* may also have two generations at this locality. Interestingly, Baker found no *Pasites* before July, whereas my observations at Jalagir were made in May at which time my party collected many adults. Obviously, more data need to be gathered to elucidate this situation.

DISCUSSION AND CONCLUSIONS

The above information reveals that the mode of parasitism of the *Pasites* is characteristic of other Nomadinae. Female *Pasites* enter the open cells of the host and implant one or more eggs in the cell wall while the host female is foraging (hence *Pasites* eggs in still-open cells of *Pseudapis*). The *Pasites* egg hatches after the host female has provisioned the cell, oviposited, and closed the cell. The parasite first instar crawls from its chorion to the provisions and kills the young host (in

this case an early larval instar). (With almost all Nomadinae either the egg or the early instar of the host is eliminated; the only exception known is that of *Protepeolus* and *Diadasia* [Rozen et al., 1978], in which the first instar of *Protepeolus* assassinates the penultimate larval instar of *Diadasia* as it is about to molt to the last instar.)

Popov (1951) divided the Ammobatini into two tribes on the basis of male genitalia and apical sterna, as follows: Pasitini includes *Pasites*, *Morgania* (and the subgenus *Omachtes*), *Pseudopasites*, *Sphecodopsis*, *Pasitomachtes*, and *Pseudodichroa*; the Ammobatini encompasses *Ammobates* (including the subgenera *Caesarea*, *Xerammobates*, and *Euphileremus*), *Parammobatodes*, and *Oreopasites*. However, the interrelationship and limits of these genera are uncertain because of the limited number of specimens in collections, the widely dispersed types, and a general confusion in the literature. The present study shows that both *Pasites* (Pasitini) and *Oreopasites* (Ammobatini) have a nearly identical egg deposition pattern, not found elsewhere in the Apoidea. Almost certainly a synapomorphy, it may argue against separate tribal placement for these genera. Of all the other genera, egg placement is known only for *Pseudodichroa* (Rozen and Michener, 1968), which has a nearly straight egg (not bent into a U) that also possesses a nearly flat operculum flush with the cell wall. Other tribes in the Nomadinae have various, often distinctive, forms of egg attachment, so that this matter deserves further investigation.

There is a profound difference in egg size between *Pseudapis diversipes* and *Pasites maculatus* (fig. 9), considering that the host adult is only modestly larger than that of the cuckoo bee. Most of the difference is probably due to the fact that many parasitic bees (but not all) produce abnormally small eggs (Iwata and Sakagami, 1966). Small-size parasitic eggs may have a better chance of being overlooked by host females. Nomadine parasitic bees apparently also have a larger number of ovarioles than solitary forms (Iwata and Sakagami, 1966; Rozen, in press) and this is often associated with the cuckoo bee's having a number of mature oocytes ready for deposition. There is a survival advantage for a parasitic bee to be able to deposit a number

of eggs in quick succession because it enables the parasitic female to oviposit in open host cells as soon as she discovers them. In contrast, egg deposition in solitary bees is delayed by the need of the female to construct a new cell (and lateral in some cases) and to forage for provisions between ovipositions. Hence, solitary bees often have very few mature or nearly mature oocytes at any one time.

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